

THE GROWTH AND ACTIVITY OF THE CORPORA ALLATA IN
THE LARVAL FIREBRAT, *THERMOBIA DOMESTICA*
(PACKARD) (THYSANURA, LEPISMATIDAE)

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Although the post-embryonic development of the Apterygota (including the Archaeognatha and Thysanura) is essentially continuous and progressive, it shows some abrupt changes similar to those associated with the metamorphoses of higher insects. In particular, the integument of newly hatched larvae lacks scales, although it bears setae; if scales develop, they do so either at the second molt, as in Archaeognatha, or at the third, as in most lepismatid Thysanura (Delany, 1957).

The processes of scale and bristle formation in Thysanura resemble those found in the higher insects (Schmidt, 1959; Richter, 1962). Furthermore the development of scales in *Lepisma* resembles metamorphic changes in that it appears to depend on the hormonal system of the insect (Piepho and Richter, 1959; Richter, 1962). Thus fragments of the integument from newly hatched *Lepisma*, if implanted into adults, molt when the adult molts and develop scales, suggesting that the control is humoral. However, the time that elapses between hatching and ecdysis to the fourth larval stage in *Lepisma* averages 17.8 days, as opposed to approximately 43 days for each stadium in the adult (Sweetman, 1952), so that in Piepho and Richter's experiments, the epidermal cells could have had time to differentiate independently between implantation and the subsequent adult ecdysis.

Other recent, experimental studies on the hormonal control of molting and reproduction in lepismatids have emphasized that the endocrine systems of these insects are similar in structure to those of the winged insects and that, at least with respect to the initiation of molting and the deposition of yolk, they appear to function in the same way (Yashika, 1960; Watson, 1963a, 1964a, 1965 and unpublished results; Rohdendorf, 1966).

The question therefore arises: If the development of scales in Thysanura is not a spontaneous event, is it regulated by the corpus allatum? In other words, do these ametabolous insects show an early stage in utilization of the allatal secretion as a morphogenetic agent?

The present paper describes experiments to check for the existence of humoral control over scale formation in lepismatids, and examines the physiological activity of the corpora allata during the life of the firebrat. Brief notes on the work have already appeared (Watson, 1936b, 1965). Attempts to influence scale formation in early larvae and in regenerating integument have so far yielded inconclusive results and will not be documented here.

¹ Much of the work described in this paper was carried out in the Developmental Biology Center, Western Reserve University, Cleveland, Ohio.

MATERIALS AND METHODS

1. *Experimental animals*

All experiments were performed on the firebrat, *Thermobia domestica* (Packard). Larvae and adults were reared under optimal conditions, at 37° C. and 84% relative humidity, as described in Watson (1964a).

2. *Implantations*

Implantations were carried out much as described by Piepho and Richter (1959). First stage larvae less than three hours old were anesthetized with carbon dioxide. The terminalia were removed from the abdomen and the insect was then cut across at the junction of the thorax and abdomen. The abdominal fragment was placed under 0.9% saline until implantation. An adult firebrat three to five days after ecdysis, and presumed to be on the point of initiating a molt (*cf.* Watson, 1964a), was anesthetized for one or two minutes with carbon dioxide, the abdomen was descaled and the larval fragment implanted through a slit in the third abdominal tergum; the wound was sealed with a paraffin-beeswax mixture. The adult was returned to 37° C. and 84% relative humidity.

The recipients of implants were fixed in neutral formalin at various times after implantation, and were sectioned serially for examination of the larval fragment.

3. *Histological measurements*

Studies of the corpora allata of other insects have indicated that changes in the physiological activity of the gland may involve changes in the volumes of cytoplasm and nucleus, commonly expressed as a ratio between cytoplasm and nucleus, with or without changes in the number of cells (*cf.* Pflugfelder, 1958; Scharrer, 1964). In the case of the firebrat, however, Watson (unpublished data and below) has shown that neither the nuclear diameter nor the number of cells alters during short-term fluctuations in the size of the corpora allata, fluctuations that are correlated with changes in the physiological activity of the gland.

The volume of cytoplasm in each allatal cell is therefore an appropriate measure of physiological activity; and as nuclear volume is constant, total cell volume is an equally valid index.

Firebrats in which such histological measurements were to be made were fixed in neutral formalin and sectioned serially at 4–8 μ .

(a) *Numbers of allatal nuclei*

Nuclei and fragments were counted in all sections of the corpora allata. The resulting numbers were corrected for fragmentation by the formulae of Marrable (1962).

(b) *Nuclear diameter*

The major and minor axes of the almost spherical nuclei were measured in 10 allatal cells in each of a series of 24 firebrats of various ages. An average diameter was calculated for each animal, and the individual means were averaged over the sample. The resulting average, 6.323 μ (S.E. = 0.067 μ), was used for all later calculations involving nuclear volumes.

(c) Volume of the corpora allata

Volumes were measured by summing the areas of all the sections of the corpora allata, using a squared eyepiece micrometer, and multiplying by the thickness of the section.

All other cytological statistics used in this paper were calculated from the above three measurements.

4. *The assay of allatal activity*

The juvenilizing activity of the corpora allata was assayed by a modification of the Polyphemus test (Gilbert and Schneiderman, 1960). Chilled pupae of the saturniid *Antheraea polyphemus* (Cram.) were placed at 25° C., until the first signs of epidermal retraction from the facial window indicated the beginning of adult development. Maxillae (which contain the corpora allata) or the ventral halves of heads sufficient to provide approximately 100 allatal cells (see below) were implanted into the midrib of the pupal antenna. Dorsal halves of the head, or an approximately equal volume of body tissue, served as control in the other antenna, and in later comparative experiments corpora allata from two different stages were implanted into the two antennae. The antennae of the resulting moth were scored for pupal characters on the scale of Gilbert and Schneiderman (1960). As the critical period for the action of the juvenile hormone ends shortly after retraction of the facial epidermis, the juvenilizing effect of the implant is a reflection of its secretory state at or immediately after the time of implantation.

5. *Analyses of data*

Statistical techniques referred to below are described in Siegel (1956) or Bailey (1959).

RESULTS

1. *Timetable of development*

At 37° C. and 84% R.H. growth from hatching to ecdysis to the fourth larval stage, when the scales first appear, occupies an average of 8.5 days; the mean lengths of the first three stadia, with standard errors, are 24.9 ± 0.47 hours, 69.9 ± 0.49 hours and 109.1 ± 5.14 hours. The larvae commence feeding in the third stadium, the residual yolk then being exhausted.

The sequence of epidermal events during the third stadium appears in Figure 1. At 18 hours after ecdysis, the epidermis appears inactive; mitosis follows, in most cases some time between the 18th and 48th hour, so that by the 60th hour, pycnotic epidermal nuclei are present in all larvae. Extensive RNA synthesis, as reflected by the basophilia of the trichogen and presumptive scale-forming cells, generally commences between the 18th and 48th hours, but strong basophilia may not develop until the third day. The epidermis starts to retract between 60 and 72 hours, the first scale-forming processes appear by 84 hours, and ecdysis follows approximately 24 hours later.

Thus any mechanisms influencing scale formation must act before the 48th hour after ecdysis, by which time the presumptive scale-forming cells are becoming recognizable,

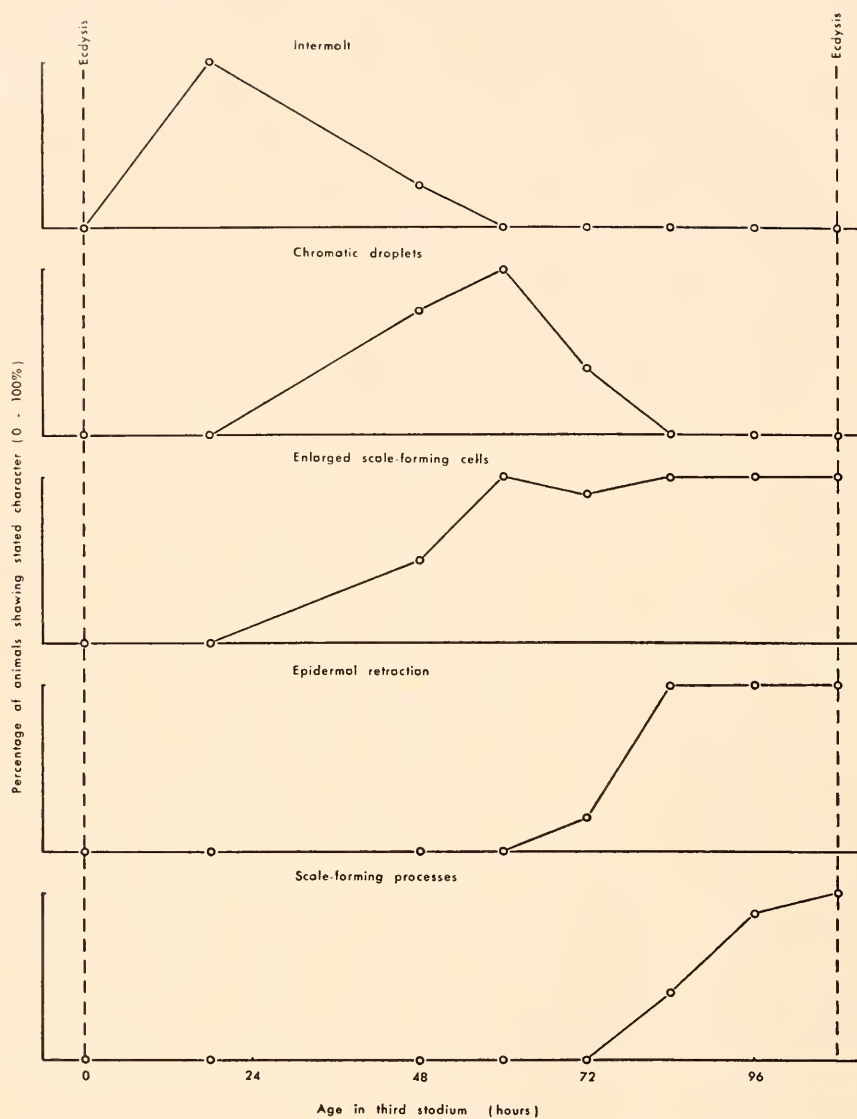


FIGURE 1. Timetable of epidermal events during the 3rd stadium of *Thermobia*.

2. Implantation experiments

The experiments on implantation unequivocally confirmed the interpretations of Piepho and Richter (1959). The implants had molted and developed scales when the adult recipients had molted, five days or more after implantation; and in a few cases, scales had formed within 48 hours of implantation (Fig. 2). Clearly, scale formation is not simply a spontaneous, time-dependent differentiation; the

potential for it is present in first stage larvae, and can be realized immediately in an appropriate environment. As some of the implants which had developed scales still contained abundant yolk in close proximity to the integument, it seems unlikely that a component of yolk directly inhibits scale formation. The "appropriate" environment may therefore be one which differs hormonally from that of the early larvae, as Piepho and Richter (1959) have suggested.

Could such a difference involve the juvenile hormone? In the present study, the histophysiological aspects of this question have been considered, particularly the pattern of growth in the corpus allatum and the secretory activity of the gland during larval and adult life.

3. *The post-embryonic growth of the corpus allatum*

(a) The number of cells in the corpus allatum

The number of cells in each corpus allatum increases as the firebrat grows. Watson (1963a), working with data not corrected for fragmentation, described linear growth in the adult corpus allatum, and it now appears that the linear relationship extends through the larval stages (Fig. 3). The fitted regression in Figure

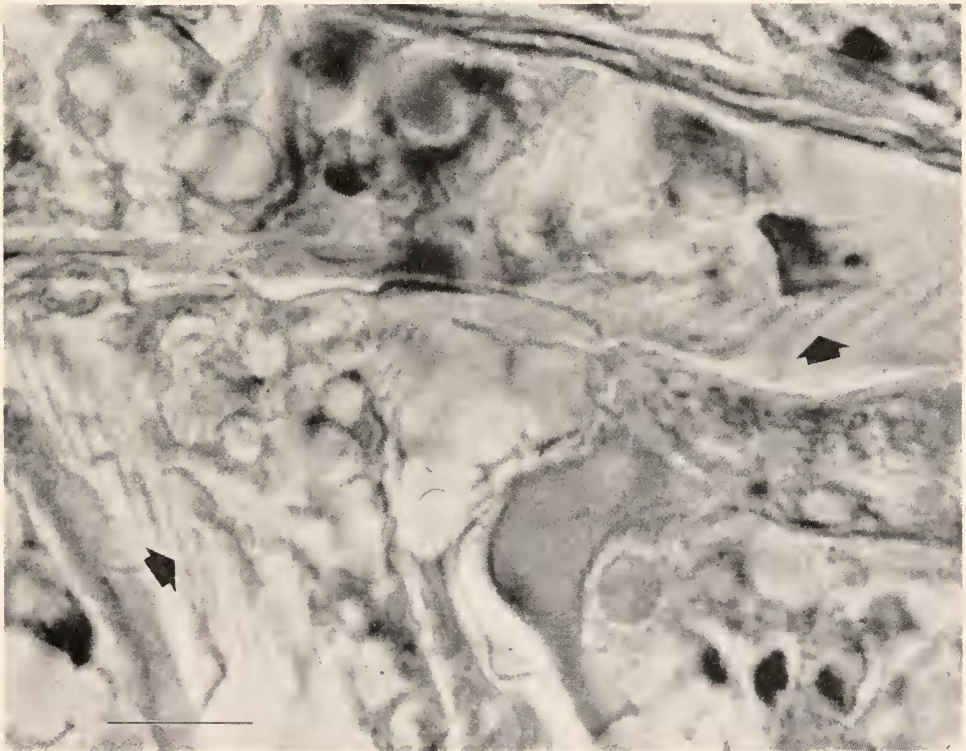


FIGURE 2. Section of integument from *Thermobia* hatchling implanted into molting adult, and left for 48 hours. The prematurely-formed scales are indicated by arrows; the marker represents 10 μ .

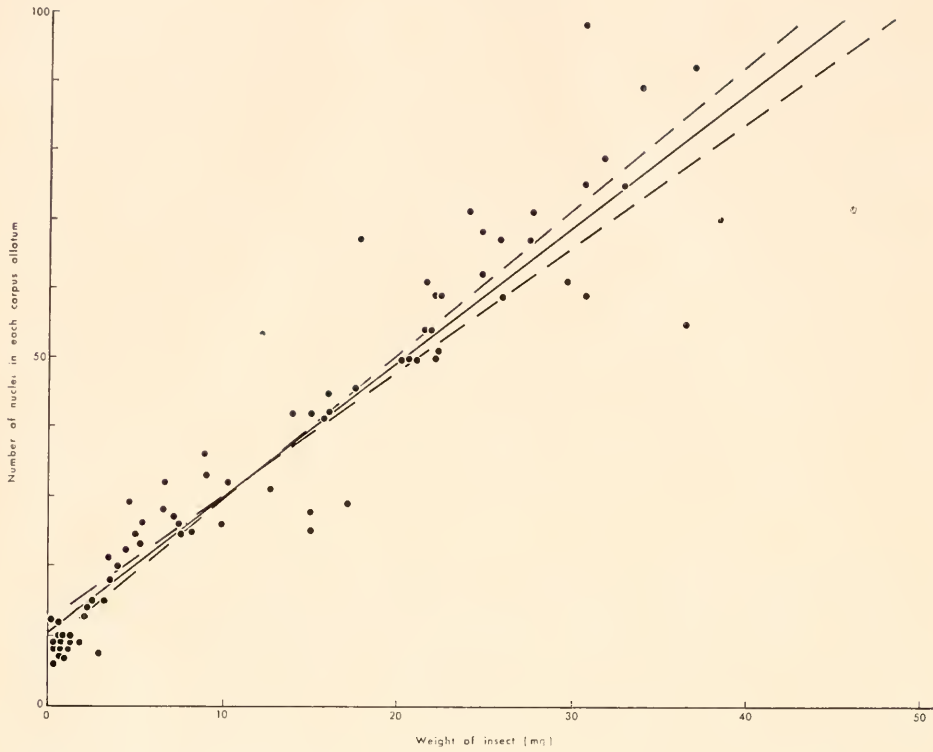


FIGURE 3. Relationship between the weight of a firebrat and the number of allatal cells. The fitted regression has the form: $y = 10.61 + 1.94x$ (modified after Watson, 1963a).

3 has the form:

$$y = 10.61 + 1.94x,$$

where y = the number of cells in each corpus allatum and x = the weight of the firebrat in mg. The 5% confidence limits for the regression coefficient are 1.80 and 2.08, so that the regression line does not intersect the origin, $P < 0.001$.

TABLE I
The numbers of allatal nuclei in larval Thermobia

Instar	Average	Range	N
1st	13.9	9.6-18.4	6
Early-mid-2nd	17.2	11.2-24.0	8
Late 2nd	16.9	15.1-18.6	5
Early 3rd	15.6	12.0-21.6	10
Mid-3rd	17.4	12.4-22.1	10
Late 3rd	18.5	14.0-23.5	5
Early 4th	16.2	12.4-18.6	6
Mid-4th	16.1	12.4-19.7	11

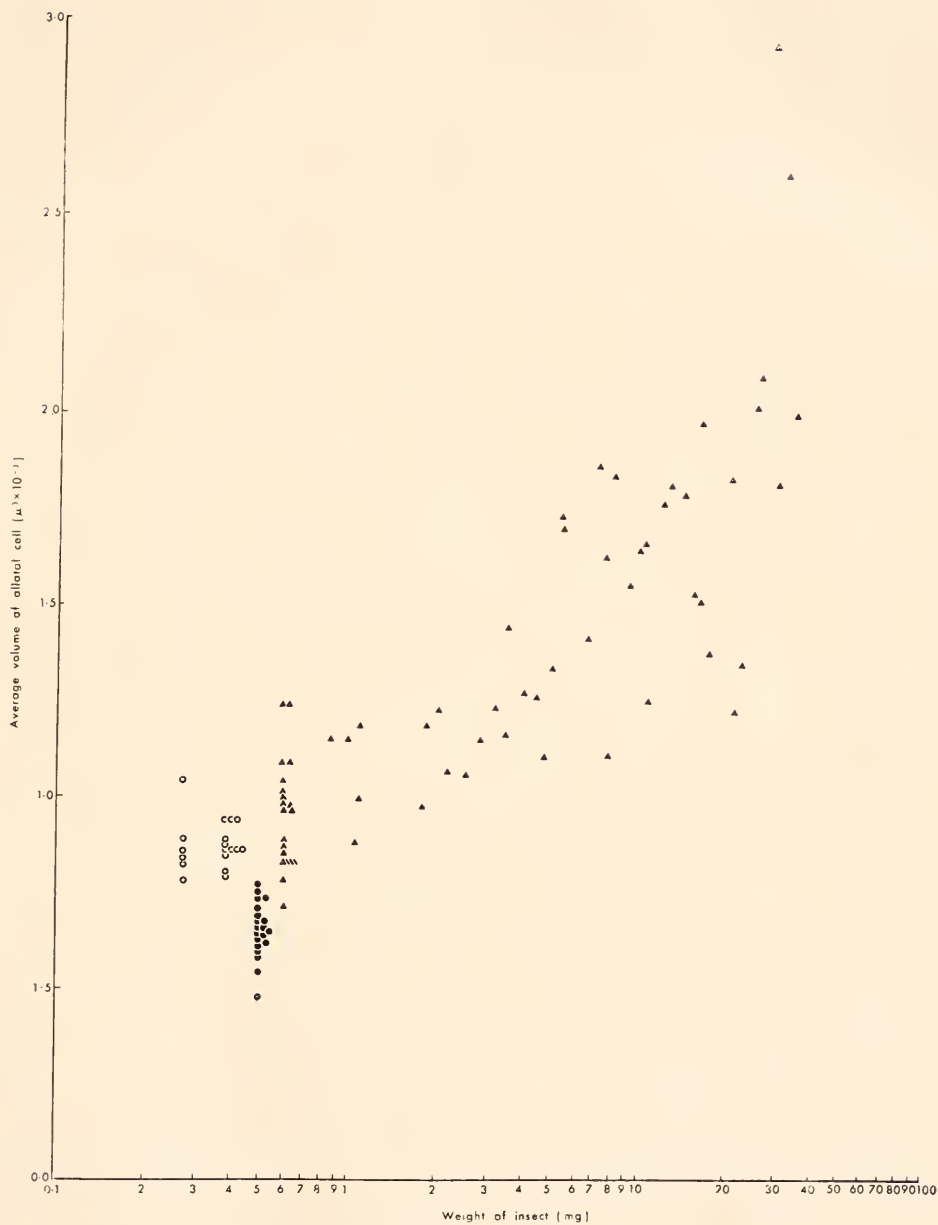


FIGURE 4. Changes in volume of allatal cells during the life of *Thermobia*. (Volumes for each of the first four instars are grouped sequentially, rather than by actual weight.) ○ = 1st and 2nd instar; ● = 3rd instar; ▲ = 4th and later instars.

Not only is the net growth in the corpus allatum linearly related to the size of the firebrat, but the growth is progressive; there are no cycles of increase and decrease within a stadium. Watson (unpublished results) has documented this for the adult, and an analysis for the first four larval stages appears in Table 1. None of the samples differs significantly from any other within that instar (Mann-Whitney "U" test).

(b) The volume of the corpus allatum

In addition to the changes in allatal volume due to the progressive increase in the number of allatal cells, there are changes due to fluctuations in the volumes of

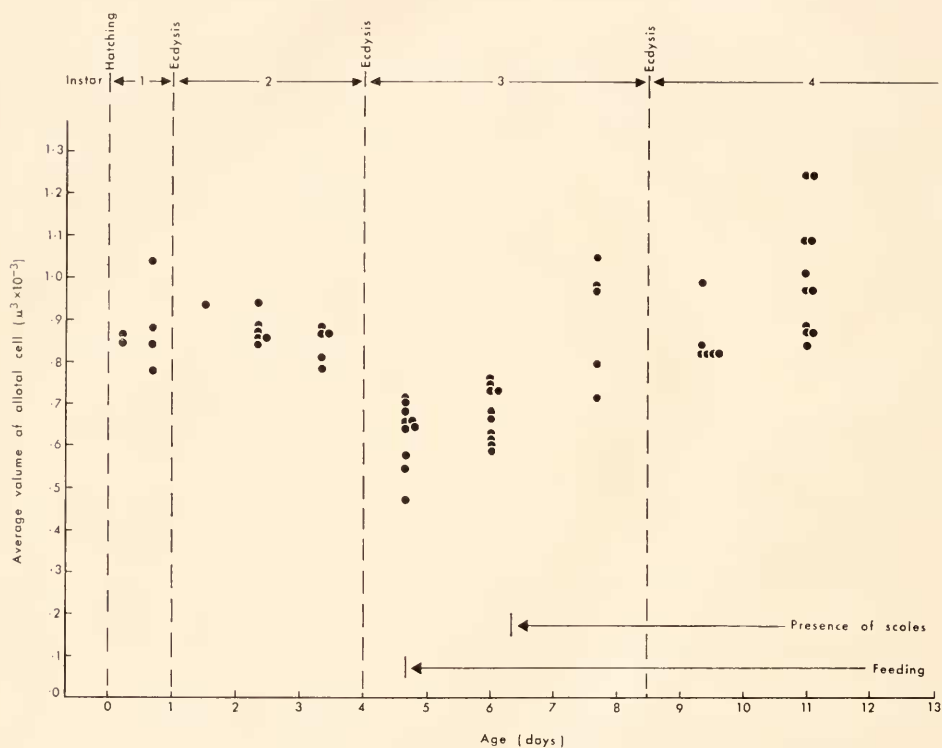


FIGURE 5. Changes in volume of allatal cells during the first four stadia of the firebrat.

existing cells. As mentioned above, these changes do not involve nuclear volume, which remains constant throughout, but depend on increases and decreases in the amount of cytoplasm. The relevant data appear in Figures 4 and 5; Figure 4 shows the period from hatching through adult life (including reproducing females) and Figure 5 presents the early larval life in detail.

The data document two points. First of all, once the scales have formed, the volume of cytoplasm in each allatal cell increases steadily until the attainment of sexual maturity. Thus the cell volumes in each of the categories, 4th instar — < 5

mg., >5 mg. — <10 mg., and >10 mg. (excluding mated females) (Fig. 4) exceed those in the previous category, $P < 0.002$ (Mann-Whitney "U" test). At weights of 8–10 mg., when the females start to mate, the cell volume may increase further, correlated with the development of the eggs (Watson, 1965 and unpublished results).

Secondly, there are changes in the allatal cytoplasm during the first four stadia. During the first two larval stages, the corpora allata maintain a constant cell volume (Fig. 5; $P > 0.10$, Mann-Whitney "U" test). After the second ecdysis, however, the volume of cytoplasm decreases; the cell volumes for early and mid-third stage larvae differ from those for first and second stage larvae, $P < 0.001$ (Mann-Whitney "U" test), as do the ratios between cytoplasm and nucleus. After the mid-third stage, when the scales have appeared on the new cuticle, the volume increases again; the cell volumes and ratios of cytoplasm to nucleus for the late third stage exceed those for the mid-third stage, $P < 0.01 > 0.001$, but do not differ from those of the fourth stage, $P > 0.10$ (Mann-Whitney "U" test).

The question then arises: Do these changes in the volume of the corpus allatum reflect changes in the physiological activity of the gland?

4. The juvenile hormone activity of the corpora allata

An initial series of assays based on the implantation of either maxillae or the ventral halves of the head into the left antenna of *Polyphemus* pupae with body or

TABLE II

The distribution of juvenile hormone activity in heads and body fragments of Thermobia

Stage of donor	Implant		No. adults emerged	L + ve	R + ve	L > R
	L. antenna	R. antenna				
1st	Ventral head	Body fragments	11	6	2	5
4th–5th	Ventral head	Body fragments	13	7	0	7
Adults	Maxillae	Dorsal head or labium	4	3	0	3

dorsal cephalic tissue as control in the right antenna, showed that the corpora allata from first stage and fourth or fifth stage larvae and from young adults possess juvenile hormone activity (Table II). Measured over the entire sample, the allatal activity exceeded that shown by an equal or greater amount of body tissue ($P = 0.0154$, Fisher exact probability test). The antennae of the resulting adult moths generally showed slight to considerable thickening of the midrib in the vicinity of the allatal implant, with fusion of the barbs up to half the width of the antenna, equivalent to scores of 0 to 3 on the scales of Gilbert and Schneiderman (1960). In the right antenna, only bodies from the first stage showed any juvenile hormone activity. In no case was there any general, systematic effect such as Yashika (1960) obtained with *Ctenolepisma*, but Yashika implanted far greater quantities of allatal tissue, and into the abdominal hemocoel.

The experiment was then extended to assay the activity of early larval corpora allata. The ventral halves of five heads were implanted into each antenna, a different instar being used as donor for each side. The antennae of the resulting adult

were scored as above, and the differences between the two antennae were analyzed by a sign test; the magnitude of the differences was disregarded, as the scoring table is based on an ordinal scale.

The results appear on Table III. As the Table shows, the corpora allata reach their minimal activity early in the third stage; the activities of the first and second stages do not differ from each other; and there is a marked rise in activity between the third and fourth stages. Thus the juvenilizing activity of the corpus allatum is related to the volume of cytoplasm in the gland. In other words, the activity of the corpus allatum is minimal at the time that scale formation is induced.

5. *The regulation of the corpus allatum*

The coincidence between the exhaustion of yolk reserves and the minimal activity of the corpus allatum suggests that the two may be connected; the activity of the

TABLE III
Juvenile hormone activity in the corpora allata of early larval Thermobia

Comparison		L < R	L = R	L > R	Interpretation and probability (Sign test)
L. antenna	R. antenna				
1st	2nd	6	4	1	2nd \geq 1st: $P = 0.062$
2nd	early 3rd	1	3	7	2nd $>$ early 3rd: $P = 0.035$
early 3rd	late 3rd	8	1	2	Late 3rd \geq early 3rd: $P = 0.055$
early 3rd	4th	11	1	0	4th $>$ early 3rd: $P = 0.006$

corpus allatum may be controlled, directly or indirectly, by the quantity or quality of food.

The allatal volume was therefore measured in third stage larval firebrats that were isolated immediately after ecdysis, placed under optimal physical conditions and provided only with cellulose ("starved" firebrats). It was found that such larvae generally became moribund and died within four days, despite the fact that cellulose was ingested; none survived to molt into the fourth stage. The corpora allata were much smaller in the "starved" firebrats than in normal animals of the same age, attaining a constant minimal volume within 48–60 hours after ecdysis (Fig. 6); $P = 0.004$ (Mann-Whitney "U" test).

Third instar firebrats that had been fed on cellulose for 3 or 4 days were then fed with cereal containing protein, and the allatal volumes were measured 24, 48 and 72 hours after resumption of normal diet, and immediately after ecdysis to the fourth stage which occurs about 10 days after the second ecdysis. As the data in Figure 6 show, an increase in allatal volume followed the resumption of feeding, except in animals which had become too moribund to recover (*e.g.* low values at 48 and 72 hours). The overall reduction in allatal volume persisted at least until ecdysis to the fourth stage, at which time the corpora allata were still smaller than in control animals (Fig. 5), $P = 0.012$ (Mann-Whitney "U" test), although they exceeded the volumes at the end of starvation, $P = 0.018$ (Mann-Whitney "U" test).

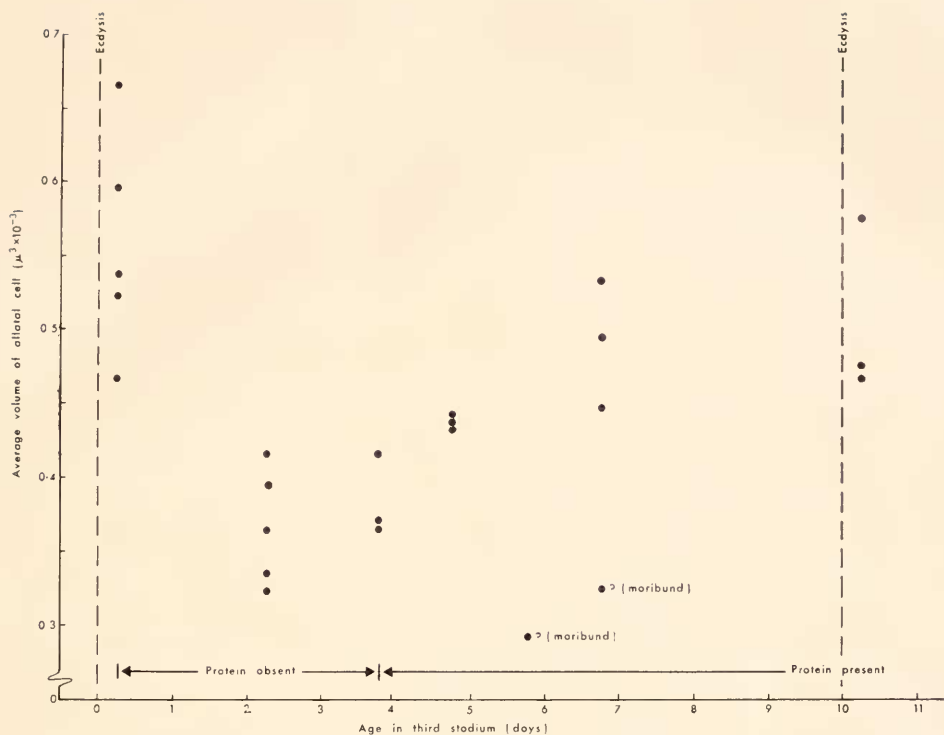


FIGURE 6. The effect of starvation on the allatal volume of 3rd instar *Thermobia*.

Thus irrespective of whether the effect of starvation is greater on the corpus allatum than it is on other tissues, it is evident that nutrition can influence the volume of allatal cytoplasm and hence, the physiological activity of the gland.

DISCUSSION

The data presented above strengthen the suggestion of Piepho and Richter (1959) and Richter (1962) that the post-embryonic development of lepismatids is regulated by changing titers of juvenile hormone. More specifically, one may correlate the appearance of scales during the third molting cycle with a precipitate fall in the activity of the corpora allata at the time of the second ecdysis, a fall possibly connected with the exhaustion of food reserves.

The question then arises: Why should scales persist when the allatal activity increases in later instars?

It is impossible to make any precise estimates of what the actual titers of juvenile hormone might be. If, however, it is assumed that the secretory potential of the corpus allatum is directly related to the volume of its cytoplasm, a supposition which is probably an oversimplification, but about which there is little critical information, it follows that the maximal titer of juvenile hormone that the gland can produce will depend on the volume of cytoplasm per unit volume of insect (*cf.*

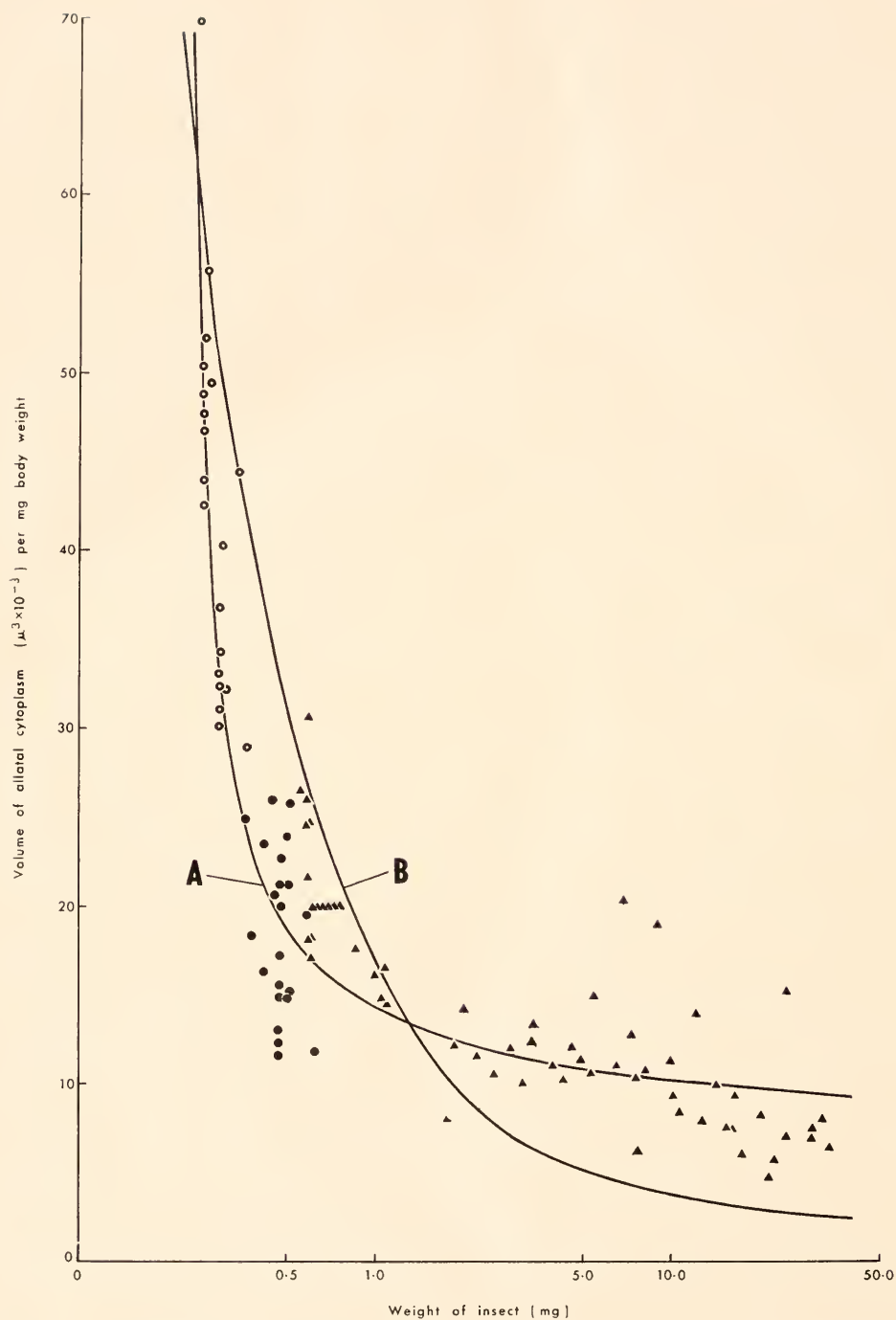


FIGURE 7. Changes in the amount of allatal cytoplasm per mg. body weight during the life of *Thermobia*. For the interpretation of curves A and B see text. Symbols as in Figure 4.

Novak, 1954). Thus in *Thermobia* the maximal titer would depend on the number of allatal cells and the average volume of cytoplasm contained in each cell. The pattern of growth in the corpus allatum ensures that the number of cells per mg. body weight decreases rapidly as the larva increases in size. At hatching, there are approximately 63 allatal cells per mg. body weight, the number of allatal cells then averaging 13.9 (Table 1) and the weight, 0.22 mg.; in the mid-late third stage, the number has fallen to approximately 41 cells per mg., the weight then averaging 0.43 mg. and the number of allatal cells, 17.7; at sexual maturity, with a body weight of approximately 10 mg., there are some 6 allatal cells per mg.; and the number approaches the asymptotic value, 3.88, in old age, at weights of 50 mg. The decline in titer that this pattern of growth could provide is shown in Figure 7B, based on the median value for the volume of cytoplasm per allatal cell ($1.358 \mu^3$) and the regression in section 3(a) above.

However, this decline is partially offset by the progressive increase in the volume of allatal cytoplasm. The observed values for the volume of allatal cytoplasm per mg. body weight appear in Figure 7 and curve A is fitted to these points. It is evident that despite the cytoplasmic changes, the range of values in the third instar is not exceeded in later larval or adult life, even in reproducing females.

Furthermore, even if the titer of juvenile hormone were to exceed the values of the early third stage, it seems probable from studies of higher insects that the dedifferentiation of the epidermal cells would not be immediate (*cf.* Wigglesworth, 1954; Lawrence, 1966). Thus inactivation of juvenile hormone from the onset of the molting cycle would prevent the prolonged exposure to the hormone which appears to be a prerequisite for dedifferentiation. It is therefore of interest that such inactivation occurs, at least in the adult firebrat; the activity of exogenous hormone (Cecropia extract) persists during the reproductive phase of the adult stadium, but not during the molting phase (Watson, unpublished results; *cf.* Watson, 1964a, 1964b).

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SUMMARY

1. The integument of the firebrat, *Thermobia domestica*, lacks scales until the molt from the third to the fourth larval stage, but retains them in all subsequent instars.

2. Implantation experiments confirm earlier findings that the scaleless integument of first stage larvae will develop scales prematurely when implanted into a molting adult, implying that the formation of scales is humorally determined.

3. The number of cells in the corpora allata increases progressively throughout the life of the firebrat, and the relationship between the number of allatal cells and the weight of the firebrat is expressed by the regression:

$$y = 10.61 + 1.94x,$$

where y = the number of cells in each corpus allatum and x = the weight of the insect in mg. The regression does not intersect the origin.

4. The size of nuclei in the corpus allatum remains constant throughout life, but the volume of cytoplasm can alter. The minimal cytoplasmic volume coincides with the deposition of the first scale-bearing cuticle. The amount of cytoplasm then increases abruptly, the level continuing to rise slowly throughout the rest of larval life. A further increase may occur in mated females.

5. The juvenile hormone activity of the corpora allata, when assayed on pupae of the silkworm *Antheraea polyphemus*, correlates with the volume of cytoplasm in the gland, and is minimal in the third stage.

6. The activity of the corpora allata is influenced by the intake of food, specifically protein.

7. Dedifferentiation of the epidermis is prevented by the pattern of growth in the corpus allatum, which indicates that the secretory potential of the gland, expressed as the volume of allatal cytoplasm per milligram body weight, is greater during the first through third instars than at any later stage, and by the inactivation of juvenile hormone during the molting cycle.

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